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A Histological Evaluation of Low Temperature Injury to Apple Trees

INJURED AND UNINJURED TREES
HIGHMOOR FARM

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CONTENTS

BULLETIN 388

A HISTOLOGICAL EVALUATION OF LOW TEMPERATURE INJURY TO APPLE TREES

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INTRODUCTION

Early in the spring of 1934 it became apparent that winter injury to apple trees (*Pyrus Malus* L.) was widespread in the commercial orchards of the State of Maine. A survey conducted during the summer of 1934 by the State Department of Agriculture showed that out of a total of 464,609 trees in 889 commercial orchards, 152,486, or 40.3 per cent, were injured. The three most severely injured varieties and their respective percentages of injury were Baldwin 69.0, Gravenstein 61.5, and Ben Davis 30.8. The McIntosh, Wealthy, and Cortland varieties proved to be relatively hardy. The percentages of injury in these varieties were 2.6, 6.7, and 8.0, respectively.

It early became apparent that orchardists were seeking a means of predicting the probable recovery of winter injured apple trees. A survey of the available literature failed to reveal a method that was either practicable or reliable. As a result an investigation was initiated with two objectives in view: (1) to determine, as accurately as possible, the histological characteristics of low temperature injury to apple trees, and (2) to develop, if possible, a method of predicting accurately the extent of recovery. The investigation and a study of the weather records together also revealed more definitely the probable time of the occurrence of the injury.

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[1] Credit is due the Coe Research Fund Committee, University of Maine, for financial aid, and to Dr. J. H. Waring, Department of Horticulture, University of Maine, for his valuable assistance and for the use of his Department's orchards.

REVIEW OF LITERATURE

Previous histological studies on plant tissues in relation to low temperature have been concerned primarily with attempts to distinguish hardy from nonhardy plants through differences in structure, such as in cell size or in the relative percentages of various elements present. Baroulina (*7*) associated large cells with hardiness, while Molisch (*38*) stated that small cells imparted hardiness to tissue. Petit (*39*) and D'Arsonval (*2*) estimated that in very small cells the water is held under considerable capillary force and that, as a result, its freezing point is lowered. Wiegand (*52*) observed that trees with small cells required lower temperatures for ice formation than trees with large cells. Rosa (*45*) found small cells characteristic of hardy plants. Rein (*42*), however, after a survey of various plant species, concluded that cell size is not related to hardiness.

English (*20*) appears to have been the first to investigate this subject in the United States. He measured the thickness of cell walls, the thickness of pith, and the thickness of bark and wood. He failed to find any relation between cell size and cold resistance. Beach and Allen (*8*) studied the relative thickness of pith and bark, the number, shape, and compactness of cutinized cells, the size and shape of collenchyma cells, and the percentage of lignified wood. They concluded that no morphological differences existed between tender and hardy species. Halsted (*23*) concluded that no constant difference probably exists among apple trees by which one sort may be distinguished from all others, or hardy from tender varieties.

Several investigators have described the histological characteristics of winter injury. Wood (*53*) noted a killing and disintegration of cortical, wood ray, and pith cells in young currant canes. Older portions evidenced cambial degeneration which was followed by a gradual degeneration of cortical and phloem tissue. He states that this allowed air to penetrate the tracheae, rendering them functionless, and that this in turn separated the tissues and caused the outermost pith cells to degenerate. Mix (*37*) recorded a browning of cell contents in apple trees which had been frozen. Woycicki (*55*) recorded the occlusion of vessels by a gum and illustrated both this and the formation of suberized tissue by the cambium following winter injury. Harris (*25*) has described some anatomical char-

acteristics of winter injured wood, but was interested primarily in "frost ring" formation in hardwoods. Rhoads (*43*) described and figured "frost ring" formation in conifers.

A further review of the literature is included in a later section describing "frost ring" formation in apple trees.

METHODS

In some of the commercial orchards of the State, in the Agricultural College orchard at Orono, and in the Agricultural Experiment Station orchard, on Highmoor Farm, at Monmouth, many trees were found showing varying degrees of injury. Trees of several varieties were chosen at the two experimental orchards for further study. Samples were taken at successive intervals during 1934 and 1935 to ascertain the nature of winter injury and the degree of recovery of winter injured trees. These samples were supplemented from trees of other varieties in commercial orchards.

The same branches of these trees were sampled at successive dates. A twig consisting of at least 3-year-old wood was removed in each case. Samples of these twigs were preserved in formalin-acetic acid-alcohol mixture until used in the laboratory. The samples taken in June, 1934, were embedded in celloidin and sectioned with a sliding microtome. The remaining samples taken in September, 1934, June, 1935, and September, 1935, were placed in 10 per cent formalin and sectioned with a sliding microtome without further treatment, except for being washed in water to remove the excess formalin. All sections were cut at a thickness of 8 to 15 microns. In cutting, the technique given by Averell (*3*) and Garland (*21*) was followed. The staining schedules given by Durand (*19*), Vaughan (*51*), Ridgway (*44*), Boyce (*9*), Dickson (*16*), Diemer and Gerry (*17*), Hubert (*30*), Cartwright (*13*), Bailey (*4*), and Stockwell (*49*) were used, primarily as a check on fungous invasion.

In November, 1934, twigs at least two years old of eight varieties in the Agricultural College orchard at Orono were sampled and frozen in an artificial freezing chamber similar to that described by Hildreth (*28*). These were allowed to thaw for three days in tap water, and were then sectioned and the sections examined for

the degree of injury. During December, January, and February, twigs of eight other varieties as well as of the same varieties utilized in November were similarly frozen and examined. In all these tests, a small portion of the twig, never more than 2 inches in length, was cut from near the end of the sample, placed in tap water, and used as a check. The remainder of the twig was placed in the controlled freezing chamber for approximately 48 hours.

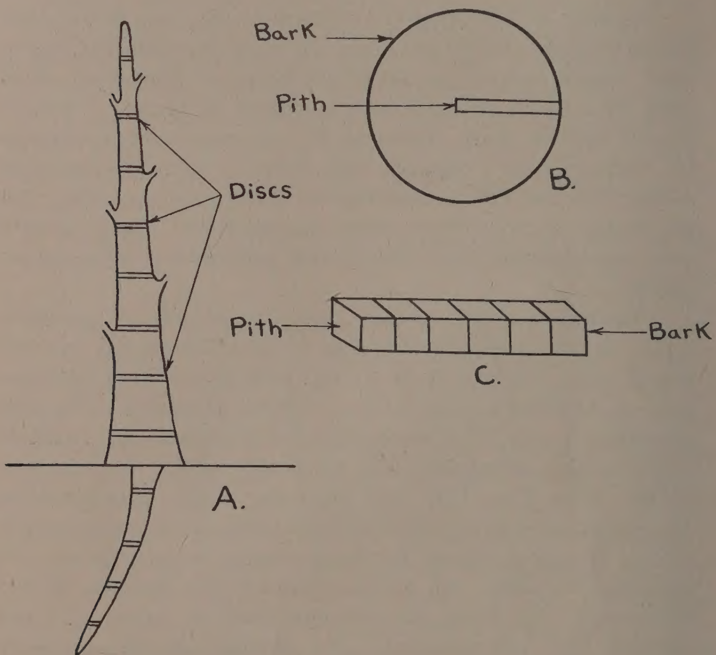


Fig. 1. Diagram of the method used in sampling an entire tree.
A.—Discs taken every 25 cm.
B.—Method of taking a segment from each disc.
C.—Segment split into convenient pieces for sectioning with the microtome.

Representative winter killed trees of four varieties in the Agricultural College orchard, and of four other varieties in other orchards of the State, were chosen to be sampled at successive in-

tervals along the main axis of the tree. The varieties in the College orchard were McIntosh, Northern Spy, Wealthy, and Delicious. These trees ranged in age from 11 to 30 years. The trees were cut down near the crown and sampled as follows. The central branch of the tree was selected as representing the entire aerial portion of the tree. All other branches were removed. Beginning at the terminal bud, a sample was taken every 25 cm. The stump was pulled and the sampling continued every 25 cm. along a major root to its tip. Each sample consisted of a disc about 2.5 cm. thick, representing a cross section of the tree at each 25 cm. These discs were sawn so that a small segment about 2.5 cm. thick by 1.2 cm. wide was taken extending from the bark to the pith. This segment was then split into convenient pieces suitable for sectioning. The procedure was carried out so that the slides, when completed, represented a series of radii of a tree, from the pith to the bark, taken every 25 cm. from the terminal bud to the end of a major root. Fig. 1 illustrates the method.

RESULTS

General and Histological Effects of Winter Injury

Baldwin is the outstandingly nonhardy commercial variety grown in Maine, and exhibits all types of winter injury. In many orchards of this variety, complete killing of fruit and leaf buds occurred. (See Plate 1, A.) Some badly injured trees of this variety produced foliage, but the leaves soon withered and died. In other cases subnormal foliage developed in the spring and lasted the entire season, but the trees did not produce leaves the next year. Many trees were found in which some of the branches developed almost normal foliage, while other branches on the same tree had only small, subnormal leaves. (See Plate 2, A and B.) The microscopic examination of both kinds of branches from the same tree showed an occlusion of the vessels by a substance resembling wound gum in those branches bearing subnormal foliage. In no case, examined histologically, was there any evidence of a killing of the cambium. Recovery apparently depended upon the development and maintenance of sufficient foliage to promote growth. In a Baldwin tree (Plate 2, A.) two branches were selected. One, near the top

of the tree, had almost normal foliage. Upon microscopic examination on June 15, 1934, it was found that the cambium had formed one complete row of xylem elements and part of a second row. Some killing was evident in the wood rays and wood parenchyma, resulting in the loss of some stored food materials, but the vessels were unobstructed. (See Plate 4, B.) Recovery was rapid, and by September, 1934, the branch was as normal in external appearance as any branch on an uninjured tree. A second branch on this tree, near the base of the branching system, produced small, underdeveloped leaves. Upon microscopic examination it was found here also that the cambium was entirely free from any injury, and by June 15, 1934, it had formed as much new xylem as the first branch sampled on this tree. However, the proportion of wood rays and wood parenchyma cells killed was much greater than in the other branch. The vessels were occluded by a substance resembling wound gum, and only a few were open for the conduction of water. (See Plate 4, A.) Re-examination of this branch in September, 1934, showed that death was almost complete, and by July, 1935, death was complete as evidenced by the drying and peeling of the bark. The same results were obtained from a study of the King David tree shown in Plate 2, B, and the Gravenstein tree shown in Plate 1, B. Similar results were also obtained from a study of trees of the Wealthy, Northern Spy, and McIntosh varieties, in other orchards.

It was soon evident that the degree of injury was related to the number of occluded vessels and killed parenchyma cells. Apparently either may bring about the same external symptoms. Sections of branches injured in these ways are shown in Plate 4, A-D, and Plate 5, A-D.

The samples taken during September, 1934, and June and September, 1935, were examined to determine the extent of recovery from low temperature injury. As mentioned previously, the degree of injury appeared to be related to the numbers of occluded vessels and killed parenchyma cells, which together form what is termed "black-hearted wood." Trees were selected that showed both extremes, that is, those that had branches which externally seemed completely recovered, and those that had branches which externally appeared completely killed. Samples were taken of the wood, where it was at least three years old, and histological sec-

tions made. These were examined to determine the percentage of parenchyma cells killed and of vessels occluded by gum. The killed parenchyma cells were readily recognized without staining, as the protoplasts were brown and disorganized. In every case, the presence of a nucleus was taken as the criterion of life. This is illustrated in Plate 5, A, in which one cell near the center of the field was undoubtedly uninjured, while the remainder of the cells show very definite disorganization of the contents.

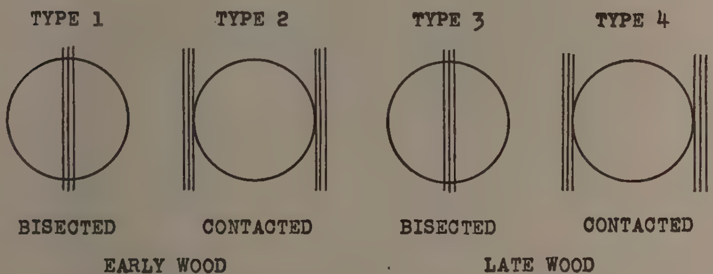


Fig. 2. Types of fields selected for statistical analysis of the ratio of parenchyma cells to other types of wood elements in the secondary xylem of varieties of apple trees.

In order to discover how to obtain comparable results, in comparing trees or parts of a tree, a preliminary microscopic analysis was made. As apple wood contains both uni- and multiseriate wood rays, microscopic fields of four types were selected, as illustrated in Fig. 2. Two types were bisected by a multiseriate wood ray, and two others were contacted by two multiseriate wood rays. Bisected and contacted fields in the early and late wood were selected. All of the cells in each microscopic field were counted. The data from a total of ten fields of each type were recorded. The ratio of the total number of parenchyma cells to cells of other elements was calculated, and comparisons were made by Student's method. The results are given in Table 1.

As shown in Table 1, the location of the wood rays is important, but not the time of wood formation. Therefore comparison should be made between trees or parts of a tree with the ray in a definite place in all fields.

TABLE 1

Statistical analysis of cellular elements in the secondary xylem of apple wood

Kinds of fields compared[1]	Odds[2]
Early wood, bisected vs. contacted	81:1
Late wood, bisected vs. contacted	37:1
Bisected, early wood vs. late wood	1.59:1
Contacted, early wood vs. late wood	1.58:1

[1] The one given first had a higher percentage than the other, of cells consisting of parenchyma.
[2] Odds of 30 or more to 1 are considered to be significant.

An examination was made of branches, from four varieties, that were completely killed, or that died during the growing season of 1934. From these same trees, branches also were examined that, although injured, recovered during the growing season of 1934. The resulting data are given in Table 2. From this table it is evident that if approximately 50 per cent of the vessels are occluded the branch probably will not recover, but if only 20 per cent are occluded, recovery is probable. If approximately 50 per cent of the parenchyma cells are killed the branch probably will not recover, but if only 25 per cent are killed, recovery is probable. In any one series of samples, the two kinds of injury appear to be alike in percentage of vessels occluded and parenchyma cells killed.

TABLE 2

Percentage of occluded vessels and killed parenchyma cells in the secondary xylem of apple varieties injured in 1933-34

Variety	Condition	Per cent of vessels occluded	Per cent of parenchyma cells killed
Baldwin	Killed	61.02	55.38
Baldwin	Recovered	17.02	26.81
Red Astrachan	Killed	54.73	58.06
Red Astrachan	Recovered	22.69	22.50
King David	Killed	48.73	48.75
King David	Recovered	19.85	23.43
Wealthy	Killed	53.02	57.31
Wealthy	Recovered	28.19	31.62

It is generally accepted that for growth during the first few weeks of each season, the tree is dependent upon the reserve food stored in the parenchyma cells. After the leaf area has nearly reached its maximum for the season, the tree depends more and more upon currently elaborated food. Thus if some stored food is available to the cambium so that the tree develops sufficient new growth, recovery is possible. Sufficient food will be available to the cambium only if some of the parenchyma cells are still alive and the xylem is able to conduct water, i.e., if the vessels are not occluded by gum, or if enough new conducting xylem is formed. Plate 4, C and D illustrate the type of recovery found in Wealthy and Red Astrachan. In both cases, the occlusion of vessels is evident, but the percentage of killed parenchyma in the two fields illustrated is very low. It appears highly probable that in these two cases, enough stored food was available for new growth, and because new conducting xylem was produced, the tree recovered.

The relationship between the killing of parenchyma and the occlusion of vessels is even more apparent if we consider a possible method of formation of this gum. During the microscopic analysis it was noticed that vessels occluded by gum always had parenchyma cells adjoining them. These parenchyma cells always contained a brownish substance resembling the gum occluding the vessels. Broekhuizen (*11*) has shown that, in elm twigs, the formation of gum is a metabolic process resulting from various types of injury to parenchyma cells. It is believed that the protoplasts of these cells respond to the external stimuli by forming gum, which gradually penetrates into the vessels through the pits between the parenchyma cell and the vessel. As discussed in a later section, it is possible to produce this occlusion of the vessels by artificial freezing.

Gradual Decay by Fungi

The susceptibility of blackhearted wood to fungal activity has been noted by many investigators. The fungi found fruiting on severely injured trees have in general been saprophytes or facultative parasites. *Polyporus tulipiferus* (Schw.) Overh. and *Schizophyllum commune* Fr. were the most common. Fruiting bodies of *Peniophora cinerea* (Fr.) Cooke, *Coryneum foliicolum* Fuckel, *Phoma mali* S. and S., *Sphaeropsis malorum* Pk., *Nectria sp.,* and

Stereum purpureum Pers. were also found. In many cases trees have succumbed to fungus disease without blackheart being present. A Northern Spy tree in the orchard at Orono survived the severe winter with no apparent injury, except for a small "frost boil" in the bark of the trunk. Upon microscopic examination fungous hyphae were found in the three year old wood. This is illustrated in Plate 4, E and F. Unfortunately, the wood from which these sections were prepared was placed in formalin before the hyphae were found, and as a result, no cultures could be made to determine the fungus. It is very evident, however, that it is parasitic in action, as the wood rays show no injury other than that caused by the fungal hyphae.

DEAD PATCHES OF BARK ON THE TRUNKS

In the spring of 1934 and of 1935, particularly the latter, many trees showed dead patches of bark on the trunks, as illustrated in Plate 3, A, B. In some cases the injury took the form of a fissure, the first stages of which are shown in Plate 5, F. These dead patches of bark are due primarily to mechanical disturbances. According to Sorauer (*47*) frost will contract the tissue in direct proportion to the thickness of the walls of the cells making up the tissue. The bark suffers considerably more than the wood. Tangential contraction, tending to decrease the circumference, is much greater than radial, which tends to decrease the diameter, and this results in a differential strain. Rhoads (*43*) states that with the action of frost there must take place everywhere, within a woody axis, a preponderance of tangential strain over radial contraction, which may result in a splitting of the tissue along the wood rays. Sorauer also states that the outer cells of the primary bark are not as elastic as the underlying thin walled ones because of the greater thickness of their walls. Thus the permanent stretching will be the greatest in the outer cells of the primary bark. As a result the circumference of the inner surface of the bark is larger than that of the woody cylinder and the bark is raised up in patches. This preponderance of tangential strain frequently results in a radial cleft in the phloem which has in turn been filled in by meristematic parenchyma cells within the phloem. (See Plate 5, F.)

LABORATORY FREEZING TESTS AND CORRELATION OF RESULTS WITH OUTDOOR TEMPERATURES

The laboratory method of artificial freezing to determine the relative hardiness of varieties has been used by many investigators. Hildreth (*28*), Hill and Salmon (*29*), Ackerman (*1*); Martin (*34*), Maximov (*35*), Tumanov and Borodin (*50*), Quisenberry (*40*), Salmon (*46*), and Worzella (*54*), all obtained a high correlation between field observations of hardiness and the results of artificial freezing in the laboratory. The freezing equipment used in this study was essentially the same as that used by Hildreth (*28*). It did not, however, have as accurate control of the temperature so that a variation of a degree would sometimes occur during the freezing.

Trees of eight varieties from the College orchard were sampled on November 15, 1934. These were placed in the freezing chamber and exposed to —30°C. (—22°F.) for 3 hours. The freezing chamber was so regulated that the temperature dropped about 5° per hour. After being thawed they were sectioned and compared with the checks. The injury observed is recorded in Table 3. It is interesting to note the differences, in the region of the injury, between the two hardiest varieties available, Duchess and McIntosh. In general, it was found that the outermost cells of the pith and what remained of the primary xylem were the first to show signs of injury. (See Plate 5, E.) The next region to show injury was the cortex. Then, in succession, the wood rays and wood parenchyma cells, vessels (as evidenced by occlusion), and lastly the phloem parenchyma cells were killed. Death caused by freezing was not observed in the cambium.

At the present time, because of the lack of knowledge of physiological anatomy of apple trees, it is impossible to determine from Table 3 just which region of tissue, if killed, will affect the plant most. In other words, if an order of decreasing hardiness is to be determined by this means, a question arises as to whether or not McIntosh or Duchess should head the list, and then as to the relative position of the other varieties. In all the artificial freezing work that follows, the number of injured cells was taken as the criterion. Thus from Table 3 the order of hardiness was derived, which is included in Table 4.

TABLE 3

Tabular summary of killing and vessel occlusion in apple varieties artificially frozen for 3 hours at —30° C. on November 15, 1934

Variety	Cortex	Phloem		Secondary xylem			Primary xylem	Pith	Notes
		Parenchyma	Rays	Parenchyma	Rays	Vessels[1]			
NORTHERN SPY	In cells nearest the epidermis forming a ring about 5 cells wide	—	Very evident killing	About 10% of annual growth nearest the xylem	About 10% of annual growth nearest pith	Some vessels nearest pith	Some vessels occluded	In outside ring of cells nearest xylem	Enough with occlusion to give the section a brown color
McINTOSH	—	—	—	—	—	—	—	In outside ring of cells nearest xylem	—
WEALTHY	In cells nearest the epidermis forming a ring about 5 cells wide	Very evident	—	Very evident for about 10% of annual growth	Up to cambium but not in phloem	Those nearest cambium	—	In outside ring of cells and also scattered	Vessels nearest cambium were occluded
DELICIOUS	Some scattered	Some scattered	—	Very evident for about 50% of annual growth	Very evident for about 50% of annual growth	—	—	In outside ring of cells nearest xylem	—
WAGENER	Slight	Slight	Silght	Slight	Slight	—	—	Some scattered	—
DUCHESS	Slight	Slight	—	—	—	—	—	—	—
WOLF RIVER	Slight	Slight	—	—	—	—	—	Some scattered	—
CORTLAND	Slight	Slight	—	Slight for about 50% of annual growth	Slight	—	—	—	—

[1] Occlusion of vessels with gum is the result of the killing of adjacent parenchyma cells.

The examination of a Wealthy tree proved particularly interesting. After three days' thawing it was found that the outer two rows of vessels, nearest the cambium, were occluded. Again, the

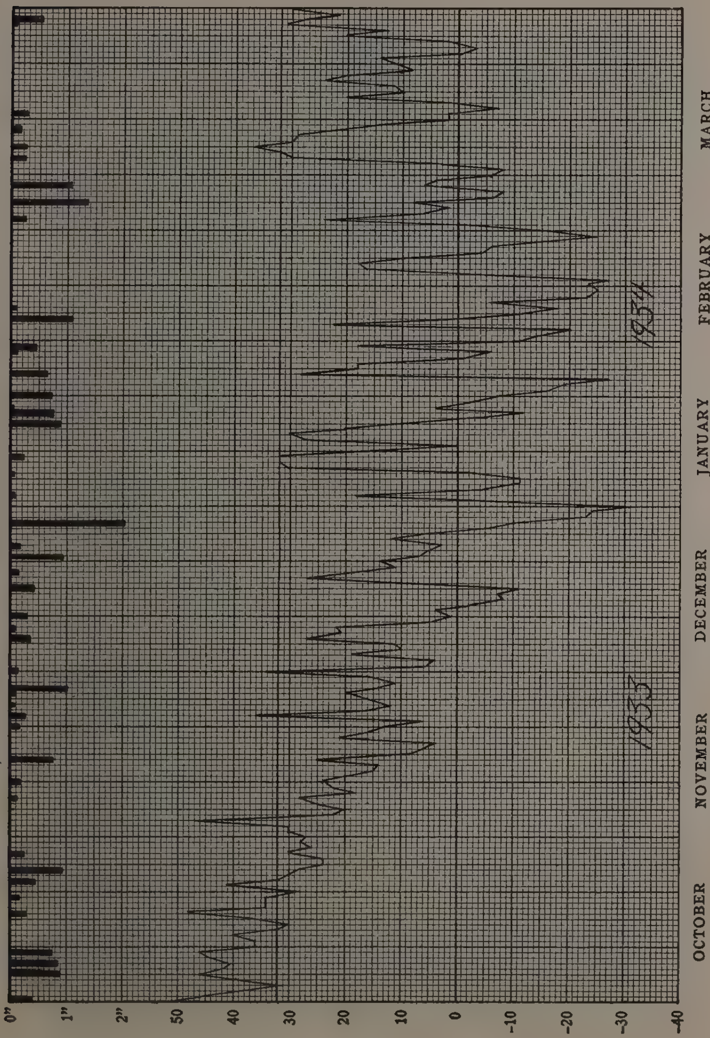


Fig. 3. The minimum temperatures and the precipitation at Orono, Maine, winter of 1933-1934.

parenchyma cells in contact with these vessels also showed a browning of their contents. Later tests showed that it was possible to produce this occlusion at any time of the year, providing that it was possible to produce the causative disorganization of the protoplasts in adjacent parenchyma cells.

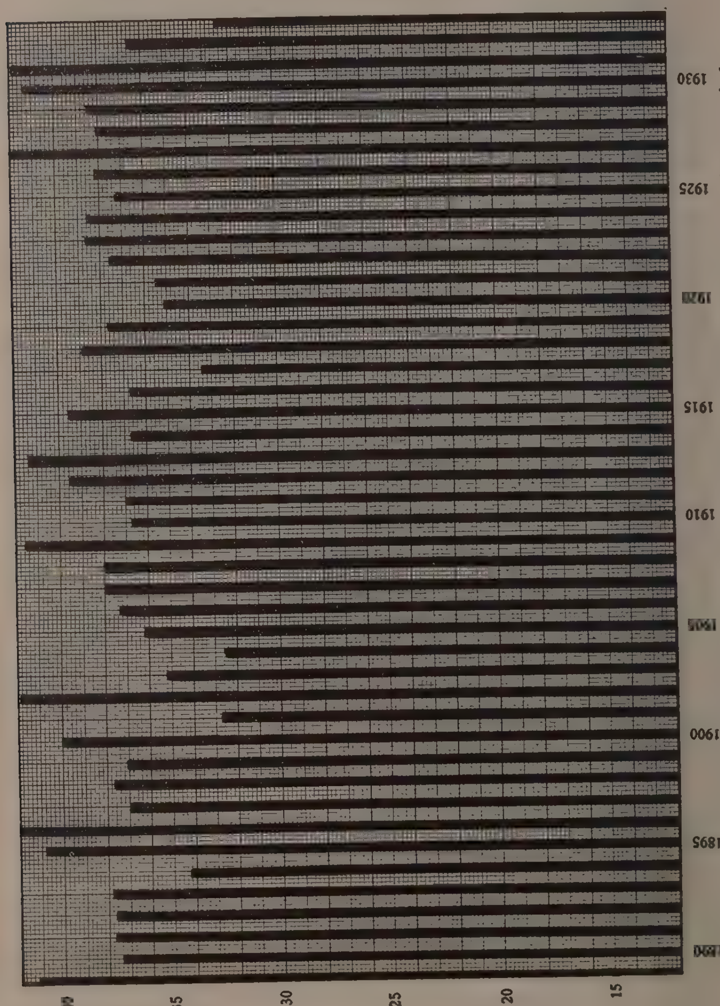


FIG. 4. The mean temperatures in the New England states for November for a 45-year period.

It is recognized that the temperature used in this November freezing is below any recorded for November at Orono. It was chosen after many trials in which it was found that it produced injury, in the Northern Spy and Wealthy varieties, that was similar to that found in the field after the winter of 1933-1934. As a mat-

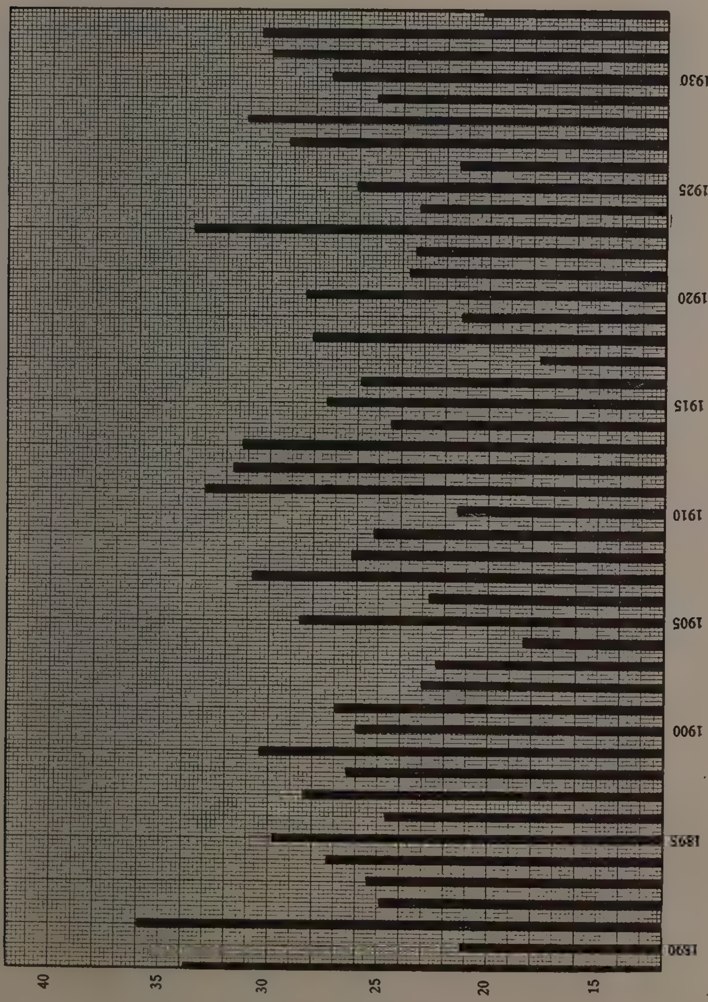


FIG. 5. The mean temperatures in New England for December for a 45-year period.

ter of reference an official low temperature of —20°F. was recorded at Van Buren, Maine, on November 29, 1933, which is 2 degrees F. higher than the temperature utilized (—30°C. or —22°F.).

Fig. 3 represents the minimum temperatures and the precipitation as recorded at Orono during the winter of 1933-1934. It is

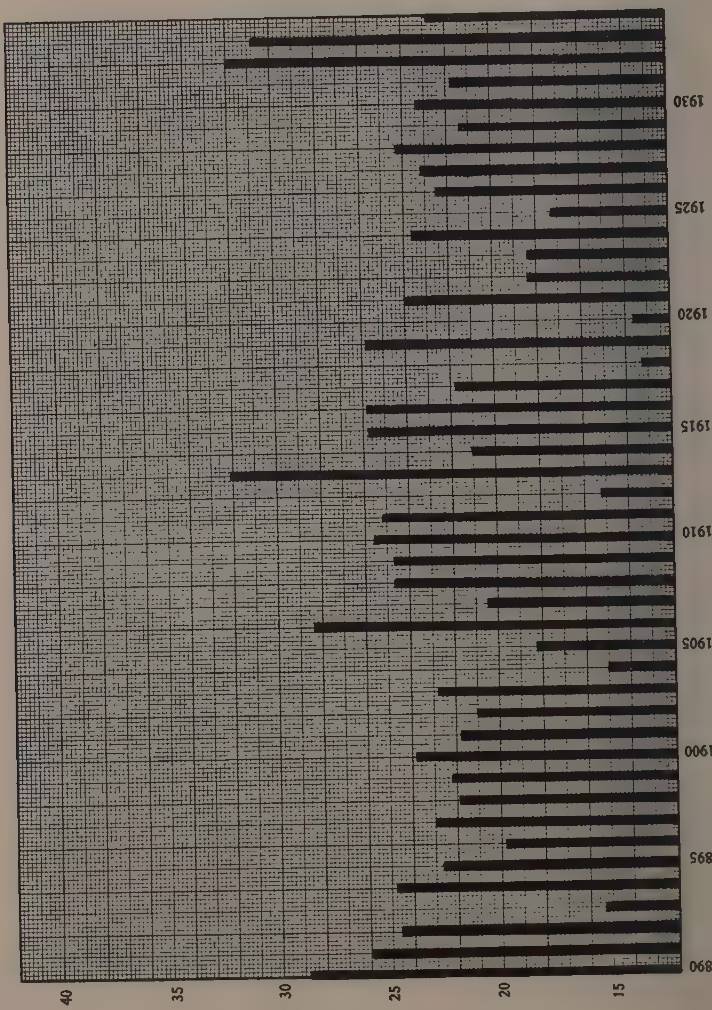


Fig. 6. The mean temperatures in New England for January for a 45-year period.

evident that in November there were only two days in which the temperature did not go below freezing. Whether or not this was an unusually cold November is disclosed when the comparable mean temperatures for November are compared with a 45-year period as shown in Fig. 4. The mean temperatures for 1901, 1904,

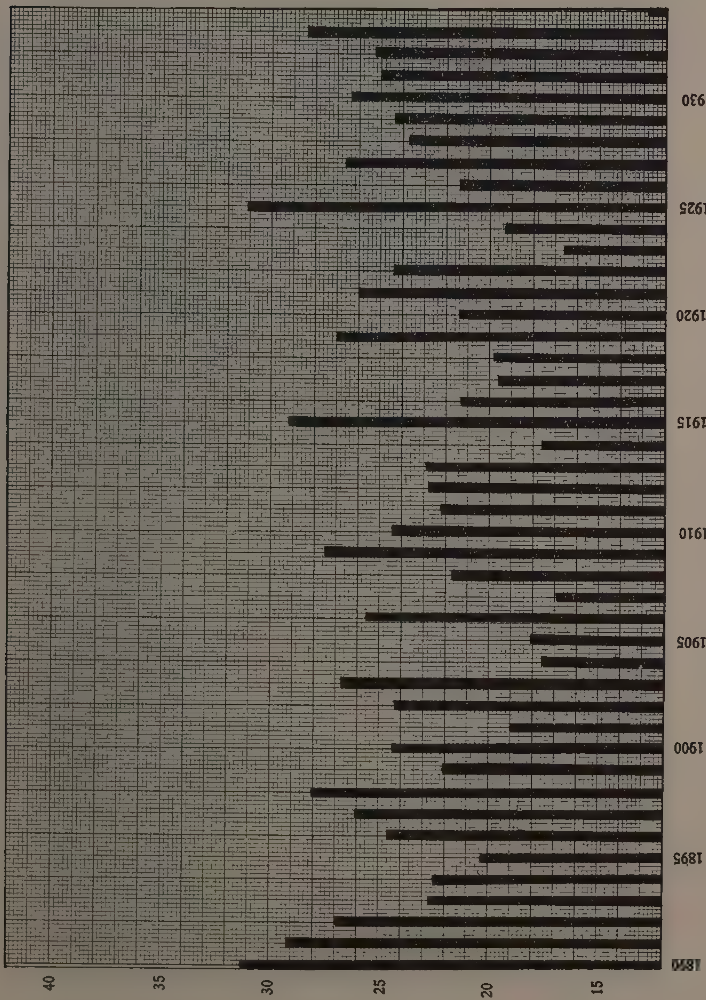


FIG. 7. The mean temperatures in New England for February for a 45-year period.

1917, and 1933, are low points in the graph. Furthermore, these four years are those in which low temperature injury was most severe and are therefore cited as test winters. Fig. 5 represents the mean temperature for December for each of 45 years. Figs. 6 and 7 show the same for January and February. These three months all show low points in many years when low temperature injury was not severe, and higher points during severe test winters. The temperature during February, 1934, however, is outstanding as it was the coldest February on record.

A further study of the weather records shows that although extremely low temperatures may have been recorded for a given day, the temperature remained at that low point for only a few hours. This is illustrated by the hourly minimum temperatures recorded at Lewiston, Maine, for December 29 and 30, 1933, two of the most severe days during the winter of 1933-1934. Although a minimum of —22°F. was recorded for these days, the temperature remained at that low point for only three hours on December 29, and for only two hours on December 30.

The results of the November, 1934, freezing tests on the eight varieties included indicate that hardening off had not progressed far enough to prevent injury in any of the varieties used. As is shown in Fig. 3, the weather conditions were not favorable for an early and gradual hardening off of the tissues. Late autumn rainfall and early low temperatures are recorded in October and November, respectively. Many references on the subject of winter injury to apple trees state that a cold night in December is the cause of the severe injury. The freezing tests conducted in November and the analysis of the weather records indicate that the injury found in 1933-1934 as well as that of previous severe winters may have occurred in November and not during the actual winter months of December, January, and February. Noting the short duration of a given period of low temperature as recorded by the hourly weather records, further artificial freezing tests were conducted, from November to April, in which apple branches were subjected to extremes they never would have received in orchard locations, i.e., —30°C. (—22°F.) for 24 hours. Injury was apparent only in November, March, and April. A tabular summary of these freezing tests and a comparison of them with field observations are included in Tables 4-6. In February, samples of other varieties

represented in various commercial orchards were frozen at the same temperature and for the same period of time, but no injury was apparent. The varieties used were: Ben Davis, Crimson Beauty, Deacon Jones x Delicious, Early McIntosh, Fameuse, Golden Delicious, Kendall, Melba, Newfane, N.W. Greening, Red Astrachan, Stark, St. Lawrence, Tolman Sweet, and Winter Banana. It is worthy of note that Ben Davis, Stark, and St. Lawrence are definitely nonhardy varieties under Maine conditions.

TABLE 4

Tabular summary of the relative order, in increasing hardiness, of apple varieties frozen artificially at —30° C. for 24 hours.

Variety	Date of freezing		Average
	3/15/35	4/15/35	
Baldwin	1	1	1
Cortland	8	13	9
Delicious	5	5	5
Dolgo (crab)	12	14	13
Duchess	11	10	11
Gravenstein	2	2	2
Haralson	7	8	7
Macoun	16	15	16
McIntosh	14	16	15
Milton	10	11	10
Orleans	9	7	8
Northern Spy	4	3	4
Stayman	[illegible]	6	6
Wagener	15	12	14
[1]Wealthy	[illegible]	4	3
Wolf River	13	9	12

TABLE 5

Tabular summary of the relative order, in increasing hardiness, of apple varieties frozen artificially at —30° C. for 24 hours on November 15, 1934, and a comparison with the corresponding rank from Table 4.

Variety	Rank	Corresponding rank from Table 4
Cortland	4	4
Delicious	3	3
Duchess	5	5
McIntosh	8	8
Northern Spy	2	2
Wagener	7	7
[1]Wealthy	1	1
Wolf River	6	6

TABLE 6

Tabular summary of the relative order, in increasing hardiness, of apple varieties from field observations and a comparison with the corresponding rank from Table 4.

Variety	Rank from field observations[2]	Corresponding rank from Table 4
Baldwin	1	1
Cortland	5	6
Delicious	4	5
Gravenstein	2	2
McIntosh	8	8
Northern Spy	3	4
[1]Wealthy	6	3
Wolf River	7	7

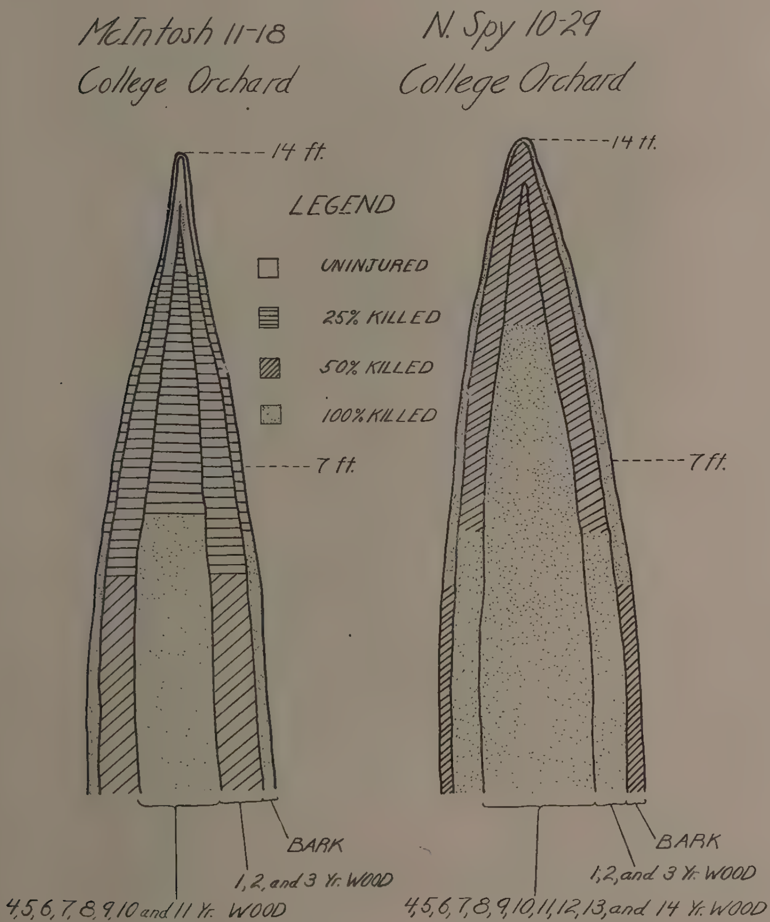
[1] The Wealthy variety at Orono was definitely nonhardy. In the rest of the State it proved to be relatively hardy.

[2] Compiled from the State Department of Agriculture Survey reports, and from field observations. Those varieties included in Table 4 and not given any rating here were not grown in large enough numbers to justify a comparison here.

HISTOLOGICAL ANALYSIS OF ENTIRE TREES

The histological examination of the segments cut from the trees illustrated in Fig. 1 gave a fairly complete picture of the degree of injury within a tree. Each year's growth in cross section was examined for killed parenchyma and occluded vessels. From these data it was possible to construct a diagram showing the relative degree of injury within different parts of a tree. Fig. 8 is representative of the data obtained on the eight varieties of trees examined by this method.

In every case the injury was greatest at the base of the tree. This is in accordance with the observations of Dorsey (*19*). The McIntosh tree shown in Fig. 8, A, was the least injured of the eight varieties while the Northern Spy shown in Fig. 8, B, was the most injured as judged from external appearances before sampling. Upon examination it was found that the only portion with no injured wood in the McIntosh was the terminal growth of the previous two growing seasons. The injury to wood then became progressively greater down the tree. The Northern Spy tree showed



A.—McIntosh.

B.—Northern Spy.

Fig. 8. Diagram of the distribution of low temperature injury within a tree, based on the analysis of histological sections of an entire tree.

severe injury. The wood at the top of the tree was 75 per cent killed, and the bark was 100 per cent killed. Injury to the trunk was much greater than in the McIntosh tree.

FROST RINGS

Abnormalities in the xylem of woody plants have been noted by many investigators. One kind of such abnormality is parenchymatous wood[2] which is wood composed predominantly of parenchyma cells. This type of malformation is characterized by the formation of isodiametric, thin walled parenchyma cells, with the cell walls heavily pitted with simple pits. The cells are usually filled with starch grains. The wood rays are widened laterally and are commonly bent and distorted. References to this parenchymatous wood are confusing inasmuch as the malformation is ascribed to several causes: cambium-mining insects, frost, drought, and lightning. The authors have noted illustrations in the literature that are essentially the same in appearance, yet ascribed to two or more different causes. For example, there is a striking similarity between the illustrations given by Rhoads (*43, p. 8, Plate 6, Fig. B.*), Day and Peace (*15, Figs. 32 and 33*), and the illustration given by Brown (*12, Plate 4*). Yet Brown's illustration is given as that of insect work, and termed a "pith-fleck," while the others are described as "frost rings." Day and Peace (*15*) state that the same kind of formation can arise from drought, and cite von Tubeuf as attributing it to lightning.

Those investigators who have illustrated and described "pith-flecks" as caused by insects have referred to the work of Kienitz (*33*), while those writing on the subject of "frost rings" have referred to Mayr (*36*). A review of the literature on "pith-flecks" is given by Record (*41*) and Brown (*12*) while the literature on "frost rings" is ably reviewed by Rhoads (*43*). Grossenbacher (*22*) has referred to a possible controversy with respect to "pith flecks," which he thinks are caused by insects, and "frost rings." He says: "...for some unknown reason these observations by Kienitz remained unfinished and became obscure; neither botanists nor entomologists seem to have paid much attention to them, and as a result some unfortunate errors have developed. Haberlandt says that medullary spots are to be considered primarily storage tissues

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[2] The terminology of Harris (*25*) is adopted here in order to prevent any confusion between wood parenchyma (parenchyma wood, parenchymholz), which is of normal occurrence, and that type of parenchyma which arises as a result of wound stimuli.

because they contain starch and tannin; while Sorauer, though giving some prominence to Kienitz's work, treats the matter under the general head of injurious or sub-optimal temperatures..." Grossenbacher's criticism of the statements in Sorauer's text which occur on pages 613 to 615 is not justified. On page 571 of this text[3] we find the statement: "...in the wood parenchyma aggregations, irregularly extended, yellow stripes are found; the yellow color arises from swollen cell walls which are universally found in frost injuries. Also, other characteristics of a definite group of frost injuries are present *as for example, the lateral displacement of the medullary ray cells*[4] at the frosted place and the barrel-shaped widening of the medullary ray where it enters the parenchyma aggregation."

Kienitz's original illustration of a "pith fleck" shows a cavity filled with isodiametric cells, with the wood rays cut off at the margin of the cavity and not extending into or through it. This is also true of the illustration of a "pith fleck" from Ratzeburg as reproduced by Grossenbacher in Plate 4, Fig. 7a. The definition of a "pith fleck" as given by the International Association of Wood Anatomists (*14*) is: "island (in cross section) of wound tissue composed of irregularly arranged isodiametric parenchyma cells occluding tunnels made in the cambium by the larvae of certain insects." This definition makes no reference to wood rays[5] extending into the cavity, such as are apparent in some of the illustrations given by investigators of "pith flecks" as caused by cambium mining insects.

Day and Peace (*15*) further add to the confusion already existing in the literature of physiological anatomy by saying that: "...both lightning and lack of water cause the formation of zones of abnormal tissue that are identical in type to the frost ring..." Unfortunately they overlooked the work of Bailey (*5*, *6*) who illustrated and described "frost rings" and defoliation injury, and also the work of Harper (*24*) which also illustrates the effect of defoliation on woody tissue. There is no resemblance between the illustrations of defoliation injury in either of these last two publi-

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[3] Dorrance's English translation of Sorauer, P. Manual of Plant Diseases, Vol. 1, Non-Parasitic Diseases, Berlin, 1908.

[4] Italics are Sorauer's.

[5] Terminology of the International Association of Wood Anatomists (*14*).

cations and the type of "frost ring" noted in this paper and illustrated in Plates 6 and 7. The illustrations given by Day and Peace in Figs. 40 and 41, as of abnormal tissue caused by drought, and compared in Fig. 42, as of abnormal tissue caused by frost, are very similar. However, the divergence from normal in all of these is too slight to permit them to be considered identical with frost rings and the abnormality due to defoliation as described by Bailey and Harper. Certainly these illustrations and those of Harper (*Plates 49 and 50*) and those of Bailey (*6, Plate 13, Fig. 2, and Plate 14*), could never be considered as identical with frost rings such as are illustrated by Mix (*37, page 281*), Rhoads (*43, Plates 2, 4, 5, and 6*), Bailey (*5, Plate II*), Hemenway (*27, p. 366*), Sorauer (*48, pp. 505, 509*), Hubert (*30, p. 112*), Harris (*25, p. 498*), Bradford and Cardinell (*10, p. 8*), and in the present paper in Plates 6 and 7.

It thus appears that several conflicting points of view exist in the literature concerning the cause of this parenchymatous wood. Sorauer (*47*) has proved experimentally that the lateral displacement of the wood rays is caused by frost, and if this is accepted as a criterion of frost injury it would differentiate that type of parenchymatous wood due to low temperature from that due to other possible causes. The original illustrations of Kienitz and Ratzeburg (as illustrated in Kienitz's article) show cavities filled with isodiametric parenchyma cells, but the wood rays do not enter the cavity. There is also no mention of the wood rays in the accepted definition of a pith fleck. This then leaves for consideration only the types of abnormalities caused by drought and lightning. Von Tubeuf, as cited by Day and Peace (*15*), introduces lightning as a cause of parenchymatous wood similar to that due to frost, but offers no experimental evidence to support this contention.

As a result of the conflicting theories, an experiment was planned to compare the effects of drought, defoliation, and frost on potted apple trees. Apple trees of seedling populations were subjected to drought and defoliation in the greenhouse during the growing seasons of 1934 and 1935, but in neither case was there any evidence of a compression of cambial cells or a lateral displacement of the wood rays. These characteristics did appear, however, in the potted trees from the same population that were artificially frozen and then placed in an environment suitable for growth. A cross section of the stem of one of these potted plants is shown in

Plate 7, F. The cambium shows very definite evidence of being compressed and distorted, while the wood rays are laterally displaced and almost approach the typical "knees" described by Hartig (*26*) and Rhoads (*43*). (See also Plate 6, F, and Plate 7, D and E.)

Following the frost theory, it is suggested by Sorauer and elaborated by Rhoads and Bailey, that the cambial cells are compressed and deformed, and the wood rays expand laterally in response to the lessening of the normal pressure of the bark on the adjacent wood elements. As water is withdrawn from the part of the living tissue inside the cambium girdle, a correspondingly thick ice mantle is formed. This dissolves in the spring, and a cavity is left between the bark and the wood. When growth is resumed in the spring, the wood rays respond to the preponderance of tangential strain by broadening laterally. This lateral displacement is illustrated in Plate 6, A, B, and D, and Plate 7, C. The cambial cells, being compressed and distorted by the ice, respond to the development of the cavity by differentiating into irregularly shaped short celled parenchyma as illustrated in Plate 6, A and B, and Plate 7, C. When the cavity is filled and the bark once more exerts its normal girdling action on the cambium, normal wood elements are formed. According to Rhoads, the severity of the ice mantle previously formed governs the amount of this parenchymatous wood, as well as the displacement of the wood rays. The authors of this bulletin have therefore agreed with Sorauer and have accepted this type of lateral displacement of the wood rays within the parenchymatous wood as a criterion of low temperature injury in woody plants. This affords a means of differentiating tissue with its constituents preponderantly parenchymatous because of low temperature from that mostly parenchymatous due to other possible causes.

Plate 6 represents injury which, in the opinion of the writers, is typically "winter injury," i.e., low temperature injury that occurred when the tree was dormant, as the parenchymatous tissue is always at the face of the late wood[5] formed the previous growing season. Rhoads designates this as being the result of either early frosts occurring late in the season when the annual increment has not matured, or of frost injury occurring during the dormant season of the year.

Plate 7 represents injury that is typically "frost injury," i.e., injury that occurred when the cambium was active. It is apparent that the time of injury may be approximated by noting the amount of normal xylem formed between the face of the late wood of the preceding year's growth and the parenchymatous wood arising as a result of frost injury. Thus in Plate 7, C, D, and E is illustrated injury that may have occurred later in the season than that illustrated in A and B. According to the criterion used by Rhoads, the greater the thickness of the ice mantle the greater the amount of parenchymatous wood, and the greater the distortion of the wood rays. Thus the severity of the injury illustrated in Plate 7, C, D, and E, was greater than that illustrated in Plate 7, A and B.

During the sectioning of the trees as illustrated in text Fig. 1, and described under "Histological Analysis of Entire Trees" an opportunity was afforded to study the longitudinal extent of the parenchymatous wood. According to Rhoads the extent of the abnormality terminated rather abruptly as older portions of the tree were reached. This was also recorded by Hartig (*26*) and Kienholz (*32*). In the tree of the Wealthy variety sampled in the College orchard at Orono, the parenchymatous wood formed after the winter of 1933-1934 first appeared 200 cm. below the terminal bud. It continued for 100 cm. more, reaching its maximum at approximately 69 cm. from the point where it was first observed. At 125 cm. or a total of 375 cm. from the terminal bud it was no longer in evidence. In the tree of the McIntosh variety from the same orchard the parenchymatous wood extended for about 125 cm., and again it was first observed about 200 cm. from the top of the tree. Plate 6, A and B illustrates the formation in these two trees. The figures given for these two are illustrative of the data obtained on the eight trees in this series. In a tree of the Baldwin variety from this same series, the parenchymatous wood was found in the early wood (thus representing frost injury) of 1905, 1922, 1924, 1926, 1928, and 1931. It also appeared on the face of the late wood (thus representing winter injury) in 1906, and 1918. No growth was made in 1934 as the tree was completely killed the preceding winter.

SUMMARY

The effects of low temperature injury to *Pyrus Malus* L. are apparent first as death of the protoplasts in the parenchyma cells. This is followed by an occlusion of the vessels by a substance resembling wound gum. The killed parenchyma cells and occluded vessels together form what is termed "blackhearted wood."

The ultimate recovery of apple wood injured by low temperature is apparently dependent upon the development and maintenance of sufficient foliage to promote growth. Environmental conditions are often a determining factor. Anatomically this is possible only if some storage cells remain alive and the xylem remains capable of conduction after the period of low temperature. In no case was the dormant cambium found to be injured, even after artificial freezing when the branches were subjected to a lower temperature than was ever recorded in the orchards.

In this series of studies microscopic examination of the woody tissues of branches showed that if approximately 50 per cent of the vessels are occluded the branch probably will not recover, but if only 25 per cent are killed, recovery is probable. If approximately 50 per cent of the parenchyma cells are killed the branch may not recover, but if only 20 per cent are killed, recovery is probable.

Artificial freezing experiments indicated that the injury found after the severe winter of 1933-1934 occurred in November of 1933, and not during the winter months. The definitely nonhardy varieties, such as Baldwin, were injured if frozen during November, but if permitted to harden off they could withstand lower temperatures than ever recorded by authoritative weather records. A study of weather records disclosed that severe test winters were characterized by periods of low temperature in November.

A review of the literature revealed at least four casual agencies of abnormal parenchymatous wood. By definition and by original illustrations in source material there should be no confusion between "pith flecks" and "frost rings." The data given by some investigators to support the contention that drought can cause a similar malformation are not considered sufficient. It was shown experimentally that the compression of cambial cells and the lateral displacement of wood rays are characteristic of low temperature injury

in woody plants. If this is accepted as a criterion of frost injury it would differentiate "frost rings" from other types of parenchymatous wood. In the apple trees examined, the parenchymatous wood increased in the longitudinal axis as older portions of the tree were reached, and did not decrease as indicated by previous investigators.

LITERATURE CITED

(1) Ackerman, A.
1919. Bestimmung der Relativen Frosthärte bei Pflanzenvarietäten durch künstliche hervorgerufene Kälte. Proc. Verbe. Comm. Meteor. Agr. 3 Reum. Copenhauge.

(2) D'Arsonval, M.
1901. La pression osmotique et son rôle de défense contre le froid dans la cellule vivante. Compt. Rend. Acad. Sci. Paris. 133:84-86.

(3) Averell, J. L.
1926. Suggestions to beginners on cutting and mounting wood sections for microscopic examination. Jour. Forestry 24:791.

(4) Bailey, A. J.
1934. The penetration of fungi through wood. Jour. Forestry 32:1010-1011.

(5) Bailey, I. W.
1925. The "spruce budworm" biocoenose. I. Frost rings as indicators of the chronology of specific events. Bot. Gaz. 80:93-101.

(6) ————————
1925. Notes on the "spruce budworm" biocoenose. II. Structural abnormalities in *Abies balsamea*. Bot. Gaz. 80:300-310.

(7) Baroulina, E. I.
1923. The winter resistance of cereals. Ann. Inst. Agron. Saratov 1:42-57. (In Russian. English résumé, p. 56-57.)

(8) Beach, S. A., and Allen, F. W.
1915. Hardiness in the apple as correlated with structure and composition. Iowa Agr. Exp. Sta. Res. Bul. 21:159-204.

(9) Boyce, J. S.
1918. Imbedding and staining diseased wood. Phytopath. 8:432-434.

(10) Bradford, F. C., and Cardinell, H. A.
1922. Observations on winter injury. Mo. Agr. Exp. Sta. Bul. 56:3-16.

(11) Broekhuizen, S.
1929. Wondreaksies van hout net Enstaan van Thyllen en Wondgom in het bizonder in verband met de Iepenziekte. Doctoral Dissertation, Leiden.

(12) Brown, H. P.
1913. Pith ray flecks in wood. U. S. Dept. of Agric., Forest Service Circ. 215.

(13) Cartwright, K. St. G.
1929. A satisfactory method of staining fungal mycelium in wood sections. Ann. Bot. 43:412.

(14) Committee on Nomenclature, International Assoc. Wood Anatomists.
1933. Glossary of terms used in describing woods. Tropical Woods 36:1-12.

(15) Day, W. R., and Peace, T. R.
1934. The experimental production and the diagnosis of frost injury on forest trees. Oxford Forestry Memoir 16, 60 pp.

(16) Dickson, B. T.
1920. The differential staining of plant pathogen and host. Science 52:63-64.

(17) Diemer, M. E., and Gerry, E.
1921. Stains for the mycelium of molds and other fungi. Science 54:629-630.

(18) Dorsey, M. J.
1919. Some characteristics of open pollinated seedlings of the malinda apple. Proc. Am. Soc. Hort. Sci. (1919):34-42.

(19) Durand, E. J.
1911. The differential staining of intra-cellular mycelium. Phytopath. 1:129-130.

(20) English, L. W.
1898. The winter killing of twigs and buds. Thesis, Univ. of Vermont.

(21) Garland, H.
1935. Notes on wood section microtechnique. Jour. Forestry 33:142-145.

(22) Grossenbacher, J. G.
1910. Medullary spots: A contribution to the life history of some cambium miners. N. Y. State Agr. Exp. Sta. Tech. Bul. 15:49-65.

(23) Halsted, B. D.
1889. An investigation of apple twigs. Iowa Agr. Exp. Sta. Bul. 4:104-132.

(24) Harper, A. G.
1913. Defoliation: Its effects upon growth and structure of the wood of *Larix*. Ann. Bot. 27:621-642.

(25) Harris, H. A.
1934. Frost ring formation in some winter-injured deciduous trees and shrubs. Amer. Jour. Bot. 21:485-498.

(26) Hartig, R.
1895. Doppelringe als Folge von Spätfrosten. Forstl. Naturwiss. Zeitschr. 4:1-8.

(27) Hemenway, A. F.
1926. Late frost injury to some trees in central Kentucky. Amer. Jour. Bot. 13:364-366.

(28) Hildreth, A. C.
1926. Determination of hardiness in apple varieties and the relation of some factors to cold resistance. Minn. Agr. Exp. Sta. Tech. Bul. 42.

(29) Hill, D. D., and Salmon, S. C.
1927. The resistance of certain varieties of winter wheat to artificially produced low temperatures. Jour. Agr. Res. 35: 933-937.

(30) Hubert, E. E.
1922. A staining method for hyphae of wood inhabiting fungi. Phytopath. 12:440-441.

(31) ——————
1931. Outline of forest pathology. J. Wiley & Sons.

(32) Kienholz, R.
1933. Frost damage to red pine. Jour. Forestry 31:392-399.

(33) Kienitz, M.
1893. Die Entstehung der "Markflecke." Bot. Centbl. 14:21-27.

(34) Martin, J. H.
1927. Comparative studies of winter hardiness. Jour. Agr. Res. 35:493-535.

(35) Maximov, N. A.
1930. L'etat actuel de la question de la resistance des plantes au froid et les methodes modernes de sa determination. Internatl. Assoc. Plant Breeders Bul. 3:95-106. (English summary, pp. 104-106.)

(36) Mayr, H.
1894. Das Harz der Nadelhölzer, seine Entstehung, Vertheilung, Bedeutung und Gewinnung. Berlin.

(37) Mix, A. J.
1916. The formation of parenchyma wood following winter injury to the cambium. Phytopath. 6:279-283.

(38) Molisch, H.
1897. Untersuchungen über das Erfrieren der Pflanzen. 1-73. Jena.

(39) Petit, A.
1893. Untersuchungen über der Einfluss des Frostes auf die Temperaturverhältmisse der Böden von Verschiedener Physikalische Beschaffenheit. Forsch. Geb. Agr. Phys. 16: 285-310.

(40) Quisenberry, K. S.
1931. Inheritance of winter hardiness, growth habit and stem-rust reaction in crosses between minhardi winter and H-44 spring wheats. U. S. Dept. of Agriculture, Tech. Bul. 218.

(41) Record, S. J.
1911. Pith flecks or medullary spots in wood. Forestry Quart. 9: 244-252.

(42) Rein, R.
1908. Untersuchungen über den Kältetod der Pflanzen. Zeits. für Naturwiss. 80:1-38.

(43) Rhoads, A. S.
1923. The formation and pathological anatomy of frost rings in conifers injured by late frosts. U. S. Dept. of Agriculture Bul. 1131.

(44) Ridgway, C. S.
1917. Methods for the differentiation of pathogenic fungi in the tissues of the host. Phytopath. 7:389.

(45) Rosa, T. J.
1921. Investigations on the hardening process in vegetable plants. Mo. Agr. Exp. Sta. Res. Bul. 48.

(46) Salmon, S. C.
1933. Resistance of varieties of winter wheat and rye to low temperature in relation to winter hardiness and adaptation. Kansas Agr. Exp. Sta. Tech. Bul. 35.

(47) Sorauer, P.
1906. Experimentalle Studien über die Mechanischen Wirkung des Frostes bei Obst und Waldebäumen. Landw. Jahrb. 35:469-525.

(48) ——————
1933. Handbuch der Pflanzenkrankheiten, Band I, Erster Teil, pp. 503-522. Berlin.

(49) Stockwell, P.
1935. A stain for difficult plant material. Science 80:121-122.

(50) Tumanov, I., and Borodin, I. N.
1930. Untersuchungen über die Kalteresistenz von Winterkulturen durch Direktes Gefrieren und Indirekte Methoden. Phytopath. Zeitschr. 1:575-604.

(51) Vaughan, R. E.
1914. A method for the differential staining of fungus and host cells. Mo. Bot. Gard. 1:241.

(52) Wiegand, K. M.
1906. Some studies regarding the biology of buds and twigs in winter. Bot. Gaz. 41:373-424.

(53) Wood, J. G.
1929. Physiological derangement in vines subsequent to injury by cold. Australian Jour. Exp. Biol. Med. Sci. 6:103-105.

(54) Worzella, W. W.
1935. Inheritance of cold resistance in winter wheat, with preliminary studies of the technique of artificial freezing tests. Jour. Agr. Res. 50:625-635.

(55) Woycicki, S.
1931. Einfluss des Winterfrostes 1928/29 auf Holz und Rinde unseres Obstbäume. Gartenbauwiss. 5:48-54.

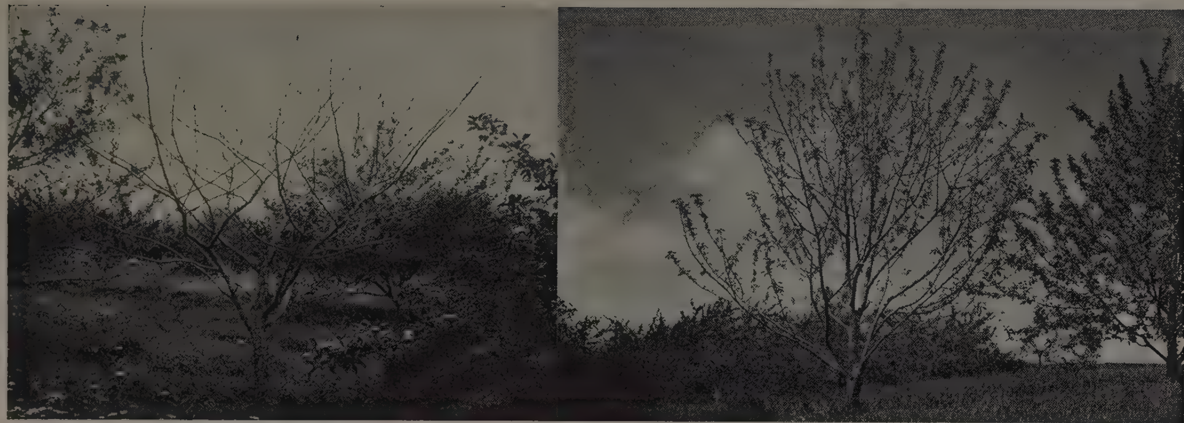

PLATE 1. A.—Baldwin tree at Highmoor Farm, photographed in June, 1934. This tree made no recovery and was completely dead at the end of the 1934 growing season.

B.—Gravenstein tree at Highmoor Farm, photographed in June, 1934. This tree recovered slightly in 1934 but died in 1935.

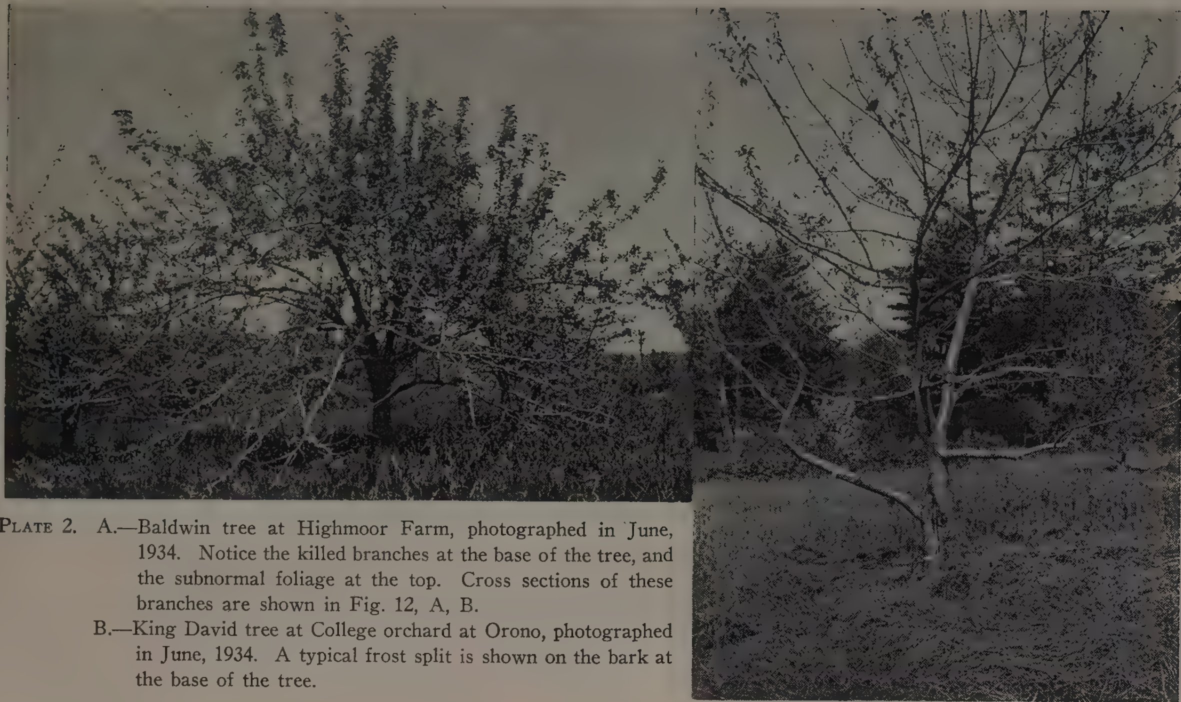

PLATE 2. A.—Baldwin tree at Highmoor Farm, photographed in June, 1934. Notice the killed branches at the base of the tree, and the subnormal foliage at the top. Cross sections of these branches are shown in Fig. 12, A, B.

B.—King David tree at College orchard at Orono, photographed in June, 1934. A typical frost split is shown on the bark at the base of the tree.

Plate 3. A.—Trunk typical of all McIntosh trees in the Agricultural College orchard at Orono. Photographed in August, 1934.

B.—Trunk typical of all Northern Spy trees in the Agricultural College orchard at Orono. Photographed in June, 1934.

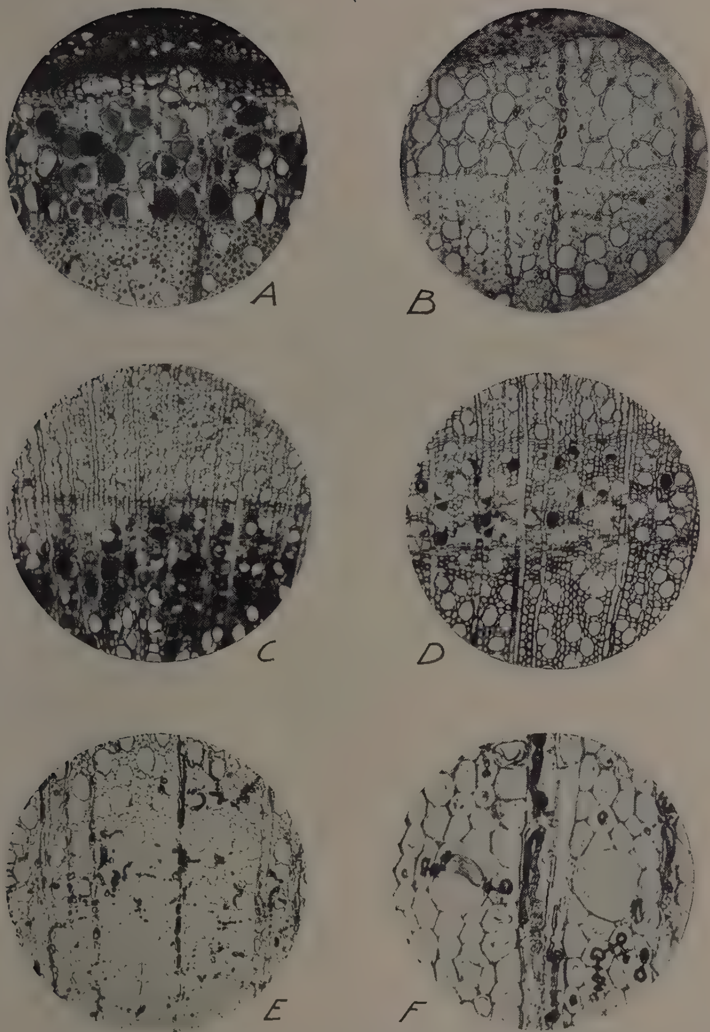

PLATE 4. A.—Occlusion of vessels by gum in a Baldwin branch near the lower part of the aerial portion of the tree illustrated in Fig. 3, A. 125x.

B.—Branch from the same tree, near the top, where some foliage was present. 125x.

C.—Recovery in a Wealthy branch; part of the annual increment of 1934 is shown at the top of the section. 110x.

D.—Same in Red Astrachan, with part of annual increment of 1932 at the bottom of the section. 110x.

E.—Hyphae in the three year wood of a Northern Spy tree. 125x.

F.—Same at 400x. Note the penetration of hyphae into wood rays that contain nuclei.

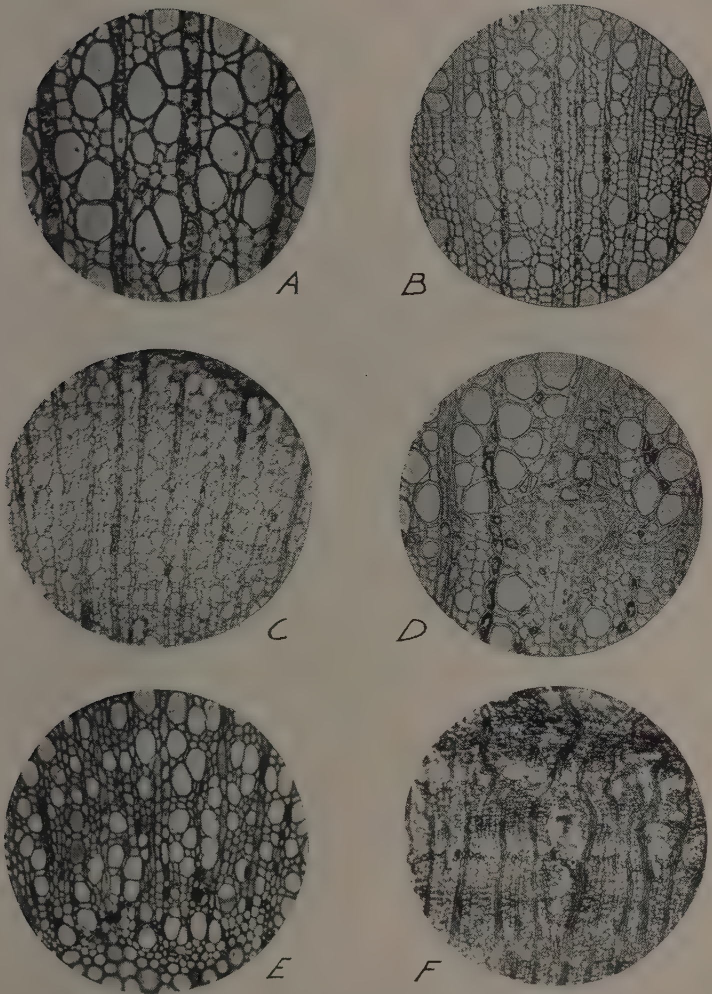

PLATE 5. A.—Killed wood ray cells. Note the living cell containing a nucleus to left of the center of the field. 125x.

B.—Killed wood ray cells in a Northern Spy tree. Portions of the xylem formed in 1932 and 1933 are shown. 110x.

C.—Killed wood ray and wood parenchyma cells in a McIntosh tree. 110x.

D.—Widening of a wood ray, and killed parenchyma in a Ben Davis. Early wood of 1934 shown at the top. 125x.

E.—Occlusion of vessels and death of parenchyma cells in an artificially frozen twig of Wolf River. 110x.

F.—Radial cleft in the phloem of McIntosh. 70x.

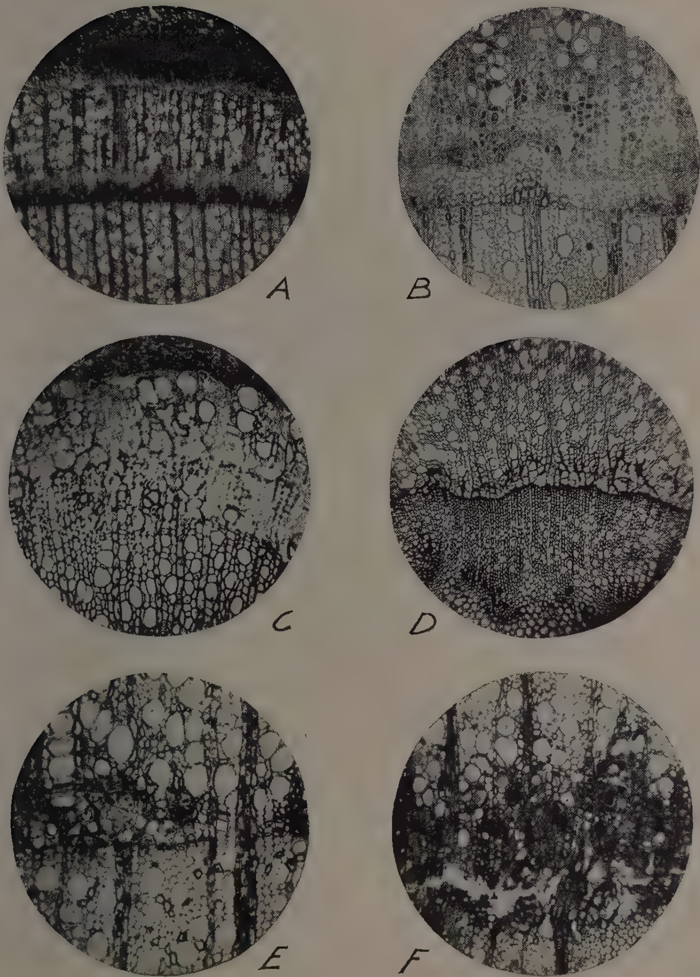

PLATE 6. A.—Parenchymatous wood in Wealthy, annual increment of 1934. 70x.

B.—Same in McIntosh, annual increment of 1934. 125x.

C.—Same in Baldwin, annual increment of 1934. 125x.

D.—Same in Northern Spy, annual increment of 1934. 110x.

E.—Same in Ben Davis, annual increment of 1924. 125x.

F.—Same in Wealthy, annual increment of 1926. 125x.

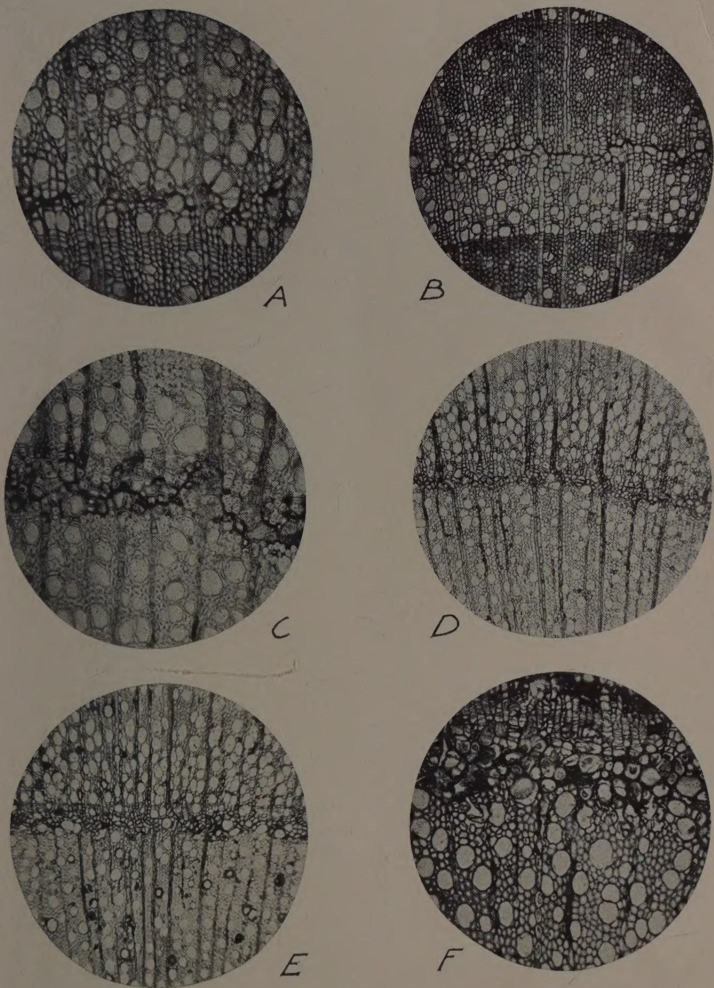

PLATE 7. A.—Parenchymatous wood in Ben Davis, early wood of 1926. 125x.
B.—Same in King David, early wood of 1931. 100x.
C.—Same in Ben Davis, early wood of 1924. 125x.
D.—Same in McIntosh, early wood of 1933. 100x.
E.—Same in Wealthy, early wood of 1934. 100x.
F.—Same in early stages of formation. In a potted Baldwin plant placed in an environment suitable for growth after freezing. 125x.